SOME NEUROHUMORAL EVIDENCE FOR DOUBLE INNERVATION OF XANTHOPHORES IN KILLIFISH (FUNDULUS)

E. F. B. FRIES

(From the Marine Biological Laboratory, Woods Hole, Mass., and The City College, New York)

Many experimental investigations during the last dozen years indicate (see Parker's review, 1940*a*) that the dermal melanophores of several teleost fishes, including *Fundulus,* are subject to the influence of both pigment-dispersing and pigment-concentrating autonomic nerve fibers and that such influence is exerted through chemical mediators. The later contributions of Chin and Li (1941), Healey (1940), Parker (1940*b*), Parker (1941), and Parker and Rosenblueth (1941) in general strengthen the case both for double innervation of the effectors studied and for chemical transmission from the nerve endings to the melanophores.

Work on other chromatophores has remained relatively scanty. In the same kind of fish one would expect to find, as Parker (1932, 1940) has assumed for the xanthophores, the same type of nervous and humoral regulation as in the melanophores. Results reported by Smith and Smith (1935) and Parker (1937) on the squirrelfish and by Dalton and Goodrich (1937) on the paradise fish support this view as regards erythrophores. Double innervation of xanthophores is implicit in Abramowitz's (1936) consideration of the neurohumors that apparently govern them. I had found that both nerves, for pigment concentration, at least, and humoral substances control xanthophore responses in the killifish *Fundulus heteroclitus* (Fries, 1931). Giersberg (1932), using partly the same methods, could demonstrate pituitary but no nervous control of the xanthophores and erythrophores in the minnow *Phoxinus,* a form in which melanophores do receive nerves, probably both dispersing and concentrating. Vilter (1939) has held that the xanthophores in another cyprinid (*Carassius*) lack nervous regulation. The possibility that certain chromatophores in some species have *single* (pigment-concentrating) innervation is suggested by work on elasmobranchs (Parker, 1936).

The present paper [1] reports further results pertaining to the nature

[1] This paper owes its origin to a small project that had attracted the interest of Dr. G. H. Parker, but which he kindly ceded to me. The work was done during two early-September stays at the Marine Biological Laboratory, Woods Hole, Mass. To the helpful officers and personnel of that institution I acknowledge grateful indebtedness.

of the nervous mechanism earlier found to control the xanthophores in *Fundulus*.

Description of Experiments

The experiments consisted basically of caudal cuts similar to those Parker (1934) devised in studying catfish melanophores. The initial, or "primary," cut (1 in Fig. 1) severed two or three fin rays with their contained nerves, etc., and with their associated interradial tissue; this cut was made at or near the distal edge of the scale-covered zone or else just proximad of the main vascular arc connecting the axial caudal blood vessels with the mostly radially arranged peripheral ones of the fin. Distal to any such cut, a yellower as well as a darker band quickly appears, characterized by pigment dispersal in both yellow and black chromatophores (Fries, 1931).[2] After a week or more, when this primary band had faded by gradual pigment concentration in consequence of the fish's response to a white or pale-blue bottom, a pair of "secondary" cuts (2 and 2′ in Fig. 1) through an appropriate span of fin-ray branches established new yellow and dark denervated bands flanking the distal portion of the primary band. These primary and secondary cuts were carried out on males and females, about 6–8 cm. long, mainly of the striped killifish, *Fundulus majalis* Wahlb., which has more distinct xanthophores than the common killifish, *F. heteroclitus* L. Externally painted glass bowls (mostly 10-inch culture dishes) with running sea water served to contain the fish and to call forth their chromatic responses to colored backgrounds.[3]

In Parker's (1934) and Matsushita's (1938) experiments on catfish melanophores, pigment dispersal in secondary bands spread into previously faded primary bands but not into intact control bands; also, responses of denervated bands to black or white bottoms occurred by gradual spread from adjacent innervated areas. Blood-borne hormones being found innocent of such spread effects, it is held (1) that pigment-dispersing nerve fibers aroused to prolonged activity by the cut are responsible for the dispersal, and (2) that these nerves act by secreting a lipid-soluble dispersing "neurohumor" that can diffuse slowly even to rather distant melanophores.

Do the xanthophores of *Fundulus* behave similarly, calling for like interpretation? Among a group of 26 *F. majalis* given secondary cuts

[2] For an account of the disposition of the yellow pigment in the xanthophores of *Fundulus*, see Warren (1932).

[3] The paints used were Carmote Colorquic white (for some dishes turned just perceptibly bluish with a trace of prussian blue), the M. B. L.'s acid-resistant black, B. Moore & Co.'s Utilac medium blue and Utilac yellow.

after the fading of successful primaries, 15 showed indications, at least once, of some spread of the yellow effect produced in bands II and II′ into the I_d half of the primary band, yet not into the N areas (Fig. 1). Several of these afforded beautifully clear demonstrations. Among them were two given a third secondary cut (2_c in Fig. 1*B* and *C*) to provide an equal innervated band (N_{cd}) as simultaneous control; no trace of

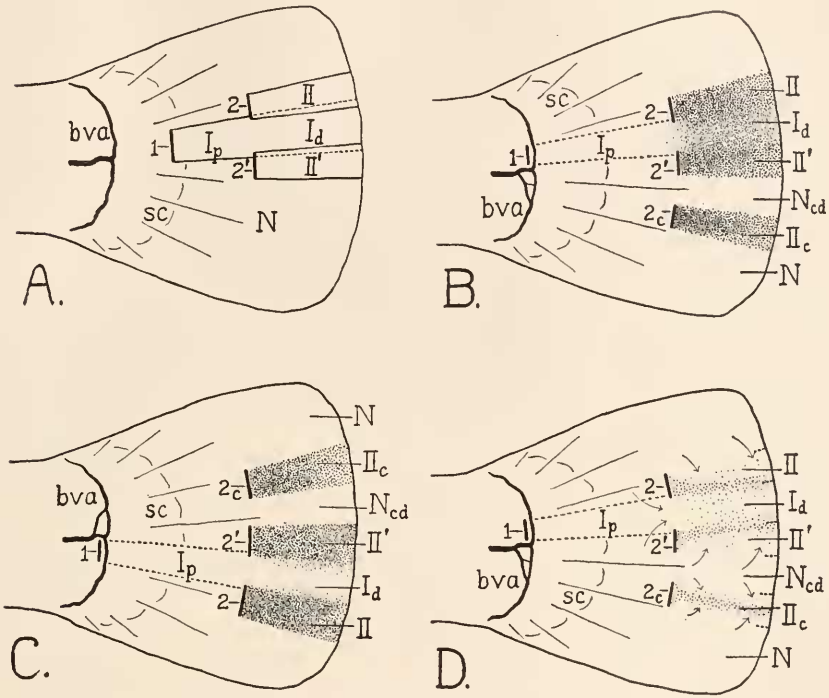

FIG. I. Diagrams of *Fundulus* tail fin. *A*. Showing denervated bands produced by transverse incisions (all cutting radial blood vessels). *B*. Showing similar bands, but including one more for control, and showing primary incision that avoids blood vessels; with stippling to indicate a good example of pronounced affirmative results. *C*. Ditto; but stippled to indicate minimum affirmative results. *D*. Ditto; but stippled to indicate loss of pronounced effect (*B*) through general pigment concentration, arrows marking progress of fading of yellow zones, or encroachment of pigment concentration from innervated zones. 1, primary cut, and I, corresponding primary band, with proximal (I_p) and distal (I_d) portions distinguished; 2 and 2′, secondary cuts, and II and II′, corresponding secondary bands; N, normal innervated regions; 2_c, additional secondary (control) cut, and II_c, corresponding secondary band, providing N_{cd}, distal normal control band; bva, blood-vessel arc of main arteries and veins; sc, distal limit of scales. Cut 1 was made dorsal or ventral to the main axial caudal vessels according as collateral supply to the arc afforded best clearance; the position of II′ and the control bands was made to correspond inversely.

spread of the yellow effect from the adjoining bands (II′ and II_c) appeared in the control bands. In these two best cases and a few others the secondary cuts were made two weeks after the primary, by which time there was extra assurance of complete degeneration of the primary-band nerves. But, because as many as 11 of the 26 showed only negative or dubious, faintly affirmative results, I took the next opportunity to carry through experiments on another set of 25 *F. majalis,* each with the self-contained control afforded in band N_{cd} by cut 2_c (Fig. 1*B* and *C*).[4]

Sleek, sound fish were selected after at least two days of acclimatization to the laboratory aquaria, i.e., after the wave of deaths that in this species often follows seining and transport. Unlike the earlier lot, the fish were fed almost daily with minced clams. The unregulated temperature of the running sea water was close to 20° C.; occasionally the fish were exposed to warmer standing water. For all tail-cutting operations the fish were subjected to cold anesthesia in an ice-and-water mixture. The best tools for the cuts had proved to be chisel-like slivers, ¾–2 mm. wide, of a Gillette-type razor blade, fastened to handles several centimeters long. The cuts were made against an enlarged glass stage under the low power of a dissecting binocular microscope after removal of any scales covering the surface to be penetrated. To assure from the outset minimum vascular differences between the innervated regions and the primary denervated band, all primary cuts, usually through two or three fin-ray bases, were made just proximad of the blood-vessel arc and close dorsad or ventrad of the main axial vessels (Figs. 1*B* and *C*). Within the hour specific note was made in which rays and interrays the nerve supply was severed, as shown by dispersal in the chromatophores which was obvious in 10–30 minutes. Usually a recheck was made on the day after the cut. At this latter time the dark and yellow band was commonly less wide than originally. Some of this loss in width may be due to the eventual dominance of uncut concentrating fibers over the influence of less strictly radially distributed cut dispersing fibers (Mills, 1932). This narrower band after fading could be revealed as a pale band by putting the fish for a few minutes over a black bottom. It may then be considered fully denervated at least in regard to any dispersing fibers. The secondary cuts 2, 2′, and 2_c (Fig. 1) were made equally long, with the same chisel, carefully oriented to adjoin the previously recorded primary band and to make bands I_d and N_{cd} equally wide; they were made eight days after the primary cut, except for five sets made six days after and six sets made ten days after. All critical determinations

[4] Though I did not know of Matsushita's (1938) work when I first applied this method to three fish in my earlier lot of experiments, he had already devised and made use of the same expedient.

of the results in the primary and control bands were made with the binocular, the fish usually being held with bare fingers. The binocular was used, too, for most other observations of the state of the caudal xanthophores, and in every instance of possible doubt. Besides some daylight (two big windows, but dark interior), illumination was by two 75-watt daylight bulbs hung in white shades two and one-half feet above the bowls and four feet apart. Under these conditions the fish changed shade greatly in two minutes when shifted between black and white bottoms and showed definite macroscopic differentiation of dorsal yellow vs. not-yellow hues in 15–30 minutes on interchange of yellow and blue bowls.

The results for the second season resembled those of the first. Among the 25 fish, carried through to one or more observations following the secondary cuts, 14 yielded affirmative indications at least once of some spread of the pigment-dispersal effect from bands II and II′ to the xanthophores in I_d but not from II′ and II_c into N_{cd} (Figs. 1*B* and *C*); four more might be included in the same category except that the proximal part (I_p) of the primary band turned about as yellow as the distal part (I_d) when the secondaries (II and II′) were formed; in three others the indications were doubtful, and the remaining four gave only negative results in the time available. One of the 25 did not withstand the operations and handling well enough to be examined for the results more than once, and the condition of the tails of several others at the inspection time was below standard. None of these poor specimens was included among the definitely affirmative 14 cases. The good cases included at least two that demonstrated the spread effect, confined to I_d, as diagrammatically as Fig. 1*B*. In the others of the 14, the effect was less pronounced, in some consisting solely of a slight transition of the xanthophore state within the edges of I_d toward the degree of dispersal characterizing the xanthophores of the adjacent II and II′ bands (Fig. 1*C*).

Among the 14 fish were 9 that failed to give the same affirmative results at some other time or times of inspection. In this connection it is well to note that the yellow spread from bands II and II′ into band I_d is rarely visible in killifish kept over a bottom inducing full pigment concentration in the xanthophores; and when it does appear, it disappears on further manipulation of the fish. Accordingly, the full count of affirmative results in both sets of experiments was obtained only by coaxing, as it were. Such "coaxing" meant that when the primary bands had faded in the fish kept in white or blue bowls, yellow bowls were substituted to induce reduction of the factors for pigment concentration throughout the tail fin. Thereby dispersal was promoted, especially in the denervated zones, and above all in the freshly formed secondary bands.

As a rule, though contrary to the indications of the obvious yellowing of the body, the innervated xanthophores in the tail fin generally got no further than the intermediate state while newly denervated xanthophores regularly attained maximum or near-maximum pigment dispersal (maintained for days over a yellow bottom).[5] In case the innervated xanthophores did show too much dispersal, the fish were again placed in a white or blue bowl to induce some reconcentration in the innervated xanthophores for the sake of better contrast with the xanthophores in the secondary bands. Sometimes several shifts of the fish from color to color were necessary to obtain the balance between dispersing and concentrating factors in the primary band permitting demonstration of the spread into it of pigment dispersal excited in the flanking secondary bands. For their strong showing of the effect even my best examples depended upon favorable adjustment of bottom colors and of factors involved in handling or exciting the fish.

Discussion of Results

Considering the whole trend of results as tallied for the two lots of fish, the evidence seems favorable to the hypothesis that xanthophore innervation includes dispersing fibers that secrete a dispersing neurohumor capable of spreading from cell to cell. In two other corroborative experiments a single flanking secondary band resulted in a spread of its yellowing effect into the faded primary band but not into the equally contiguous innervated region.

The failure of the xanthophores in intact regions to be influenced by adjacent denervated bands and their ability, not shared by denervated xanthophores, to show *prompt* adaptive response to white or blue ground color confirms the conclusion (Fries, 1931) that the xanthophores are supplied with concentrating nerves. In addition, the results in general, and particularly in their dependence on the "coaxing" procedure, accord with the view that these concentrating fibers secrete a corresponding neurohumor which, like the dispersing neurohumor, can reach more distant xanthophores by diffusing through tissue lipids (cf. Parker, 1940*b*, on melanophores). Excess of such a concentrating neurohumor, richly

[5] That the yellow bowls generally failed even in the course of more than a day to evoke full or almost-full dispersal in the xanthophores of the tail fin was contrary to prior findings (Abramowitz, 1936, for this species), yet certainly typical of the fish in these experiments—irrespective of the year or of the food supply. All observations, with rare exceptions, were begun within a few seconds after the fish had been swimming undisturbed in the bowl. Thus there was too little time for excitement or other stimuli to induce much change in the xanthophores from the condition they had assumed. The incomplete response in the tail fin to the yellow bottom color remains unexplained.

produced in innervated parts of the tail during response to a white or blue bottom and spreading into the bands, may (especially if assisted by any substance carried in the blood) fully counteract the dispersing neurohumor everywhere except at the site of its active production and consequent greatest abundance in the secondary band. Thus applied, the hypothesis accounts for rather frequent negative results in the critical tests of cell-to-cell spread of a dispersing neurohumor.

Apparently less reconcilable with the hypothesis than simply negative results was the fact that increased yellowness (pigment dispersal), resembling the spread into the denervated band from bands II and II′, appeared in the control band (N_{cd}) once in each four of the group of 25 fish. Among the four were three of the 14 that on at least one other occasion showed the spread only in the denervated band (I_d). We are concerned, therefore, not with four fish versus 14, or four out of a total of 25, but with four single instances of a phenomenon that failed to appear in more than 60 opportunities. Local equilibria of several pigment-motor factors might get mutually out of step more readily under the shifting conditions of changing bottom colors and incidental handling than with steady visual stimulation from a white bottom. This possibility may offer an adequate explanation of the four instances of yellowing of the innervated control band.

There are further reasons for holding to the interpretations involving antagonistic nerves and neurohumors. In many instances the fading of a primary yellow band obviously proceeded axipetally, i.e., beginning at the longitudinal edges, gradually extending inward, and becoming complete last in the axis of the band. In several other instances, when the intact zones became yellow after a yellow band had faded, redispersal in the band, lagging behind the dispersal occurring elsewhere, clearly took place by invasion from the edges to the axis. I could find no evidence for supposing that differences in the flow of blood, carrying typical circulatory hormones, were responsible for this mode of xanthophore change in the denervated band. When the blood flow throughout the band (cut proximad of the blood-vessel arc) was equal, as far as discernible, to that in adjacent innervated regions, axipetal change occurred as much as when the flow was obviously obstructed in bands made by distal cuts. Therefore, Vilter's (1939) explanation of lagging, axipetal band changes in terms of defective band circulation, assumed to limit renewal of local stores of intermedin, would be untenable applied to the present results. Instead, the axipetal changes in the bands conform perfectly with the view that the phases of xanthophore response depend upon different chemical and physical equilibria of the medium, that antagonistic pigment-motor nerve secretions enter into such equilibria, and that slow cellular

transmission of such secretions from active fibers is the limiting factor of xanthophore response in regions where central control of the nerves is interrupted and where there is at the same time insufficient blood-borne pigmentary hormone to swamp the effect of the nerve secretions.

Both lots of killifish supplied many examples of progressive fading of yellow secondary bands inward from the innervated edge, while progressive fading occurred along the edge next the primary denervated band only considerably later, after any prior yellow spread from the secondary bands into the primary band had been dissipated, and through gradual roundabout invasion from the innervated zones (Fig. 1*D*). The dual neurohumoral explanation is again wholly adequate. In particular the fading of either secondary or primary bands inward from adjoining innervated sectors argues for nervous production and cell-to-cell diffusion of a concentrating neurohumor.

Pigment concentration in all areas where the xanthophores exhibited any dispersal took place repeatedly as I held fish on the microscope stage for one-half to three minutes. On such occasions yellow bands, especially older ones, faded considerably, if not completely, while I watched. Sometimes, when the first inspection was limited to a few seconds, another look ten minutes later revealed that the same sort of fading had occurred and had not yet been reversed during the interval back in the yellow bowl. Frequently correlated with such quick fading of yellow bands and with equally quick concentration in innervated xanthophores was simultaneous stoppage or near-stoppage of blood flow into all sectors of the caudal fin. Resumption of circulatory inflow in the next minutes with more or less distention of veins throughout the tail was correlated with redispersal in the xanthophores that had just shown concentration, the redispersal appearing more markedly in newer bands and in innervated zones. The fact that this redispersal appeared least in old denervated bands accords with the hypothesis of a dispersing nerve secretion and the idea that activity in dispersing fibers excited by cutting diminishes after a time as the nerves degenerate (cf. Parker, 1941). Once dominated by the concentrating agents and caused to fade, such older denervated bands could not, according to the hypothesis, so quickly come to contain as much dispersing neurohumor as could innervated zones or newly excited bands.

The quick pigment concentration in both denervated bands and in innervated regions seems, on the contrary, to depend on what the blood brings. It failed to occur equally just next to rather new cuts in the fin where the blood with less effective collateral circulation was more obstructed than distally in new bands. When the circulatory change happened to be noticeably unequal in different sectors of the fin, then the

first, fastest, or greatest concentration was several times observed to occur in the xanthophores of the sector supplied at the moment with the strongest blood flow. The facts noted make it improbable that the quick pigment concentrations are due to lack of oxygen in blood (cf. Fries, 1931; Parker, 1938), which has not been found to have such a quick effect. Suspicion falls more naturally on adrenaline: it is well known to have not only vasoconstrictor action but pigment-concentrating effects on some chromatophores, and Abramowitz (1936) found that injections of an adrenal preparation evoked the concentrated condition in both innervated and denervated xanthophores of *Fundulus majalis.*

A few experiments involving primary and secondary bands, duplicating those for *F. majalis,* gave comparable results for the xanthophores of *F. heteroclitus.* Out of seven fish given secondary bands 10–15 days after the primary cut, one showed a good, and two showed some, spread of yellowing from the secondary bands into the primary between them. In two more the primary band turned yellow even in its proximal part; in the other two the results were doubtful. As far as may be judged on this basis, the xanthophores of both species of *Fundulus* evidently have identical innervation.

Though the chief recent work on teleostean melanophores, supporting the hypothesis of double innervation and of neurohumoral transmission, deals with the catfish, various evidence indicates that the melanophores of *Fundulus heteroclitus* are under essentially the same kind of nervous control (Parker, 1940*a*). It ought, therefore, to be possible to demonstrate in *Fundulus,* though Parker found the catfish better for the purpose, that a new dark band induces an adjacent denervated pale region to darken, a change consonant with the idea of an invading dispersing neurohumor. In my experiments on *F. majalis,* while primarily concerned with the xanthophores, I observed the melanophores enough to gain a well-grounded impression that, in this species, they demonstrate this about as often as the xanthophores. Unquestionably the melanophores in the faded primary band, not in the pale innervated control band, in several cases showed marked pigment dispersal between strongly darkened, flanking, secondary bands, especially next to their margins. No indications of the same phenomenon could be detected in some other cases. If double innervation and neurohumoral transmission be accepted for the killifish's melanophores on wider grounds, then the resemblance between its melanophores and xanthophores is another point in favor of accepting both concepts for the xanthophores.

What of possible alternatives? The pituitary must be considered. That it does indeed supply a hormone important for dispersing the pigment in *Fundulus* xanthophores, as suggested by analogy with *Phoxinus*

and by the results of injecting pituitrin (Abramowitz, 1936), will be shown in another paper being prepared for publication. No dispersing hormone, however, can of itself account for the spread of dispersal from the secondary bands exclusively into the distal part of the test band when dispersal is elicited in the secondaries, nor for the failures of the spread to appear at all. On the other hand, if this hormonal mechanism, probably plus an antagonistic one (adrenaline?), is thought of as co-existing with the humorally mediated double innervation, then the previously noted exceptional occurrence of dispersal in I_p as well as I_d (Fig. 1) puts little strain on the neurohumoral interpretation; such exceptions might well occur when a surplus of pituitary hormone coincides with so reduced a supply of the concentrating nerve secretion that the latter, though remaining dominant in intact regions, fails to dominate in any part of the denervated bands. Also, if comparatively reactive chromatophores in such fishes as *Fundulus* are delicately poised in relation to three or more different controlling substances, considerable variability of response is to be expected, so that other deviations from the standard spread effect would follow from excessive variations in the blood supply of the hormones or in the tone of the pigment-motor nerves.

The most plausible alternative to the thesis advocating dispersing nerves would assume co-existence of the pituitary dispersing mechanism, and perhaps a concentrating hormonal mechanism, with single innervation supplying or withholding pigment-concentrating impulses. It implies appropriate flexibility of behavior in denervated and intact chromatophores. But even if amplified to include chemical transmission from the concentrating fibers (Veil, 1936), it accounts less well than double innervation for those changes in primary and secondary bands that occur by invasion from the edges. It fails still more to account for the re-eliciting of a yellow band by recutting an already denervated but faded band (Parker, unpublished; cf. Parker, 1940*b* and 1941).

Altogether the experimental results and incidental observations, added to prior data, in my opinion support the conclusion that the xanthophores of *Fundulus majalis* and probably also *F. heteroclitus* are governed by a neurohumorally mediated reflex mechanism, including dispersing and concentrating autonomic innervation, as well as a longer-distance humoral mechanism with a pituitary dispersing hormone (presumed to be intermedin) and probably some concentrating hormone.

Summary

In a majority of over 50 *Fundulus majalis* tested, the part of a previously faded primary denervated caudal band flanked by two new secondary bands showed pigment dispersal in its xanthophores, as if affected

by the stronger dispersal in those of the adjacent secondary bands. The effect appeared whether or not the radial blood vessels were cut by the incision that produced the primary band. Intact control bands, flanked identically, generally gave no sign of a like effect.

A few experiments on *F. heteroclitus* revealed comparable responses by its xanthophores.

These observations derived from the xanthophores were paralleled by some from the melanophores in *F. majalis*.

Characteristically, slow changes in the xanthophores in response to bottom color proceeded axipetally in primary bands, and they took place in secondary bands by an analogous invasion from the edge adjoining an innervated sector rather than from the edge of the primary band.

Quick pigment concentration apparently excited by handling, holding on the microscope stage, etc., appears in denervated bands as soon as in intact sectors.

These results, certain exceptions, and other available evidence together prompt the conclusion that the xanthophores of *Fundulus* are probably controlled by nervous and humoral mechanisms involving the following components in addition to a dispersing pituitary secretion and some concentrating hormone (adrenaline?) : *A*. Double autonomic innervation, which includes (1) dispersing fibers, (2) concentrating fibers. *B*. Chemical mediation, the nerves secreting, respectively, (1) a dispersing neurohumor, (2) a concentrating neurohumor. *C*. Cellular transmission of these neurohumors to neighboring xanthophores.

LITERATURE CITED

Abramowitz, A. A., 1936. The non-identity of the neurohumors for the melanophores and the xanthophores of Fundulus. *Amer. Nat.*, **70**: 372–378.

Chin, Yin-Chang, and Ju-Chi Li, 1941. The melanophore responses of the paradise fish. *Peking Nat. Hist. Bull.*, **15**: 261–271.

Dalton, H. Clark, and H. B. Goodrich, 1937. Chromatophore reactions in the normal and albino paradise fish, Macropodus opercularis L. *Biol. Bull.*, **73**: 535–541.

Fries, E. F. B., 1931. Color changes in Fundulus, with special consideration of the xanthophores. *Jour. Exp. Zoöl.*, **60**: 389–426.

Giersberg, H., 1932. Der Einfluss der Hypophyse auf die farbigen Chromatophoren der Elritze. *Zeitschr. vergl. Physiol.*, **18**: 369–377.

Healey, E. G., 1940. Über den Farbwechsel der Elritze (Phoxinus laevis Ag.). *Zeitschr. vergl. Physiol.*, **27**: 545–586.

Matushita, K., 1938. Studies on the color changes of the catfish, Parasilurus asotus (L.). *Sci. Rep. Tôhoku Imp. Univ. Sendai*, 4 Ser. Biol., **13**: 171–200.

Mills, Sylvia M., 1932. The double innervation of fish melanophores. *Jour. Exp. Zoöl.*, **64**: 231–244.

Parker, G. H., 1932. Humoral Agents in Nervous Activity with Special Reference to Chromatophores. Univ. Press, Cambridge, Engl. 79 pp.

Parker, G. H., 1934. Color changes of the catfish Ameiurus in relation to neurohumors. *Jour. Exp. Zoöl.*, **69**: 199–233.

Parker, G. H., 1936. The reactions of chromatophores as evidence for neurohumors. *Cold Spring Harbor Symposia Quant. Biol.*, **4**: 358–370.

Parker, G. H., 1937. Color changes due to erythrophores in the squirrel fish Holocentrus. *Proc. Nat. Acad. Sci.*, **23**: 206–211.

Parker, G. H., 1938. Melanophore responses and blood supply (vasomotor changes). *Proc. Amer. Phil. Soc.*, **78**: 513–527.

Parker, G. H., 1940*a*. Neurohumors as chromatophore activators. *Proc. Amer. Acad. Arts Sci.*, **73**: 165–195.

Parker, G. H., 1940*b*. On the neurohumors of the color changes in catfishes and on fats and oils as protective agents for such substances. *Proc. Amer. Phil. Soc.*, **83**: 379–406.

Parker, G. H., 1941. Melanophore bands and areas due to nerve cutting, in relation to the protracted activity of nerves. *Jour. Gen. Physiol.*, **24**: 483–505.

Parker, G. H., and A. Rosenblueth, 1941. The electric stimulation of the concentrating (adrenergic) and the dispersing (cholinergic) nerve fibers of the melanophores in the catfish. *Proc. Nat. Acad. Sci.*, **27**: 198–204.

Smith, D. C., and M. T. Smith, 1935. Observations on the color changes and isolated scale erythrophores of the squirrel fish, Holocentrus ascensionis (Osbeck). *Biol. Bull.*, **68**: 131–139.

Veil, Catherine, 1936. Sur le mécanisme du changement de couleur chez les poissons. *Jour. Physiol. Pathol. gén.*, **34**: 824–839.

Vilter, V., 1939. Évolution de bandes sombres provoquées par la section de nerfs pigment-moteurs chez les Téléostéens. Intervention de la circulation en tant que vecteur des hormones pigmentomotrices. *C. R. Soc. Biol.*, **130**: 391–394.

Warren, A. E., 1932. Xanthophores in Fundulus, with special consideration of their "expanded" and "contracted" phases. *Proc. Nat. Acad. Sci.*, **18**: 633–639.